STROMATOPOROID PALAEOBIOLOGY AND TAPHONOMY IN A SILURIAN BIOSTROME ON GOTLAND, SWEDEN

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ABSTRACT. A well-exposed stromatoporoid biostrome in the Hemse Group (middle Ludlow) of Gotland, Sweden, displays a wide range of stromatoporoid morphologies distributed amongst 16 species. The most abundant species, *Clathrodictyon mohicanum* Nestor has a laminar to low domical form, often of large size, distributed throughout the biostrome. Fast lateral growth is suggested to account for its abundance and commonly large size, its profile being suited to the normally low to moderate energy environment envisaged for the biostrome. Several other species adopted a similar growth style but were less successful; yet others, such as *Plectostroma intermedium* Yavorskyi, show a range of growth form from low to high domical shape, suggesting a phenotypic plasticity of growth form of each of these species. However, the range simply reflects the fact that individuals grew taller with age. Most laminar to low domical stromatoporoids at Kuppen are intact, but taller forms were frequently damaged and overturned by periodic storm action, indicating that a lower profile was clearly an advantage. Some species show variations in distribution of undamaged forms horizontally between, and vertically within, localities; there is evidence that some responded to environmental gradients, notably turbulence and sedimentation. Most grew on a stable substrate provided by dead skeletons of other stromatoporoids. Under cathodoluminescence stromatoporoid skeletons show speckled dull and bright luminescence, an identical signal to the pelmatozoan debris found in the biostrome, circumstantial evidence for an original mineralogy of high Mg calcite in both.

RECENT advances in studies of stromatoporoid palaeoecology have focused attention on the importance of recognizing the degree to which genetics controlled growth form (Cornet 1975; Kershaw 1981; Stearn 1984) and this study examines these features in an excellent example of a stromatoporoid biostrome at Kuppen on southeast Gotland, Sweden (text-fig. 1). The biostrome was the subject of an earlier paper (Kershaw 1981) which demonstrated that low profile and high profile forms were created by different stromatoporoid species. However, that study was biased in its collecting, by selecting particular morphologies and at only one site on a biostrome which is exposed continuously for nearly one km laterally. Thus it was not possible to determine whether species were truly limited to particular growth forms or instead were capable of producing a range of morphologies.

In this study, a total sample of approximately 400 stromatoporoids collected from several points along the length of the biostrome provides comprehensive information on the distribution of stromatoporoids and the relationship between species and their morphotypes. Morphotypic variation is shown to be greater than that discovered in the earlier study, but is related to growth histories of individual stromatoporoids, and the interpretation of a genetic control on growth form is confirmed. Also, as the biostrome accumulated, storms selectively damaged some growth forms and certain species, and allow useful observations on the palaeoenvironment and palaeobiology of the stromatoporoids to be made. Lithification history of the biostrome and cementation of stromatoporoid skeletons are briefly examined to enhance the taphonomic interpretations. The information obtained from the study provides an insight into growth styles of different stromatoporoid species, controls on their forms, and indicates the use of stromatoporoids in determining features of the palaeoenvironment, particularly with regard to sedimentation and turbulence.

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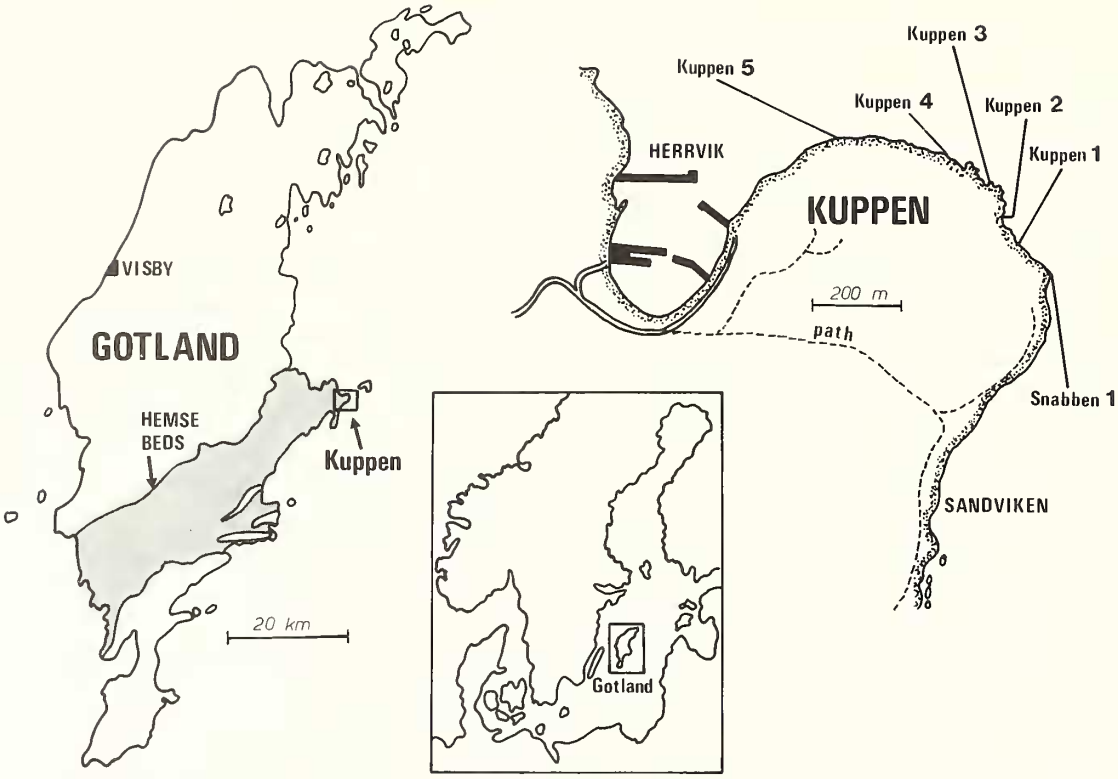


TEXT-FIG. 1. Location of the Kuppen biostrome within the Hemse Beds (stippled) on Gotland. Sampling localities are shown, details of which are filed at the Allekvia Field Station on Gotland and based on the locality system devised by Laufeld (1974*a*). Material used for this study is deposited with the Swedish Geological Survey, Uppsala.

GEOLOGICAL SETTING

The Silurian sediments of Gotland have been viewed as deposited in a carbonate platform setting (Kaljo 1970, Laufeld and Bassett 1981), but with evidence of a carbonate ramp (Frykman 1989) in the Baltic area, and record several transgressive and regressive sequences in which argillaceous limestone formations alternate with biohermal and biostromal limestones (Riding 1981).

The Hemse Beds (middle Ludlow) of Hede (1960) comprise calcareous mudstones towards the west, the Hemse Marl, and stromatoporoid-dominated biostromal and biohermal limestones in the east. The precise stratigraphic relationship between the muds and limestones is unclear. A generally southwest dipping palaeoslope has been envisaged by Martinsson (1967, p. 383) for much of the Gotland sequence, and the Hemse Marl facies are estimated to have been deposited in deeper water than the limestones (Laufeld 1974*b*). However, work with orthoconic nautiloids has shown conflicting probable shoreline trends in the Hemse Beds. Laufeld (1974*b*) interpreted current flow in their southwestern outcrops to be perpendicular to the Ludlovian shoreline which he interpreted to have an ENE–WSW trend, with open sea generally to the south. However, Sundquist (1982*a*) presented rose diagrams of bipolar nautiloid orientations for the Grogarnshuvud localities, 3 km NW of Kuppen, which show orientations at approximately 90° to Laufeld's. This suggests an approximate NW–SE shoreline in this area. These results are not necessarily incompatible because there may have been local variations in shoreline trends or current flow directions.

Shallow water facies are common in the eastern outcrops of the Hemse Beds. Ripple marks at

Gannes, 5 km west of Kuppen (Sundquist 1982*b*) are interpreted to have formed in water of about 10 m depth; Manten (1971, pp. 353, 379) reported erosion surfaces at Gannes. Cherns (1982) identified palaeokarsts, erosion surfaces and stromatolites in the overlying Eke Formation, and Cherns (1983) indicated shallow water facies at the Hemse-Eke boundary.

Biostromes 0·5 – *c.* 10 m thick are widespread in the southeast Hemse Beds, interbedded with shales, skeletal grainstones and rudstones. Such thinly bedded deposits, with shallow water associations, exhibit common vertical facies changes illustrative of a sea level fluctuating relative to sea bed. Lateral facies changes occur also, clearly demonstrable at Kuppen; there a facies mosaic is developed, termed here the Kuppen facies complex. A brief description of the complex follows, providing a background to interpretation of the stromatoporoid distributions and growth forms.

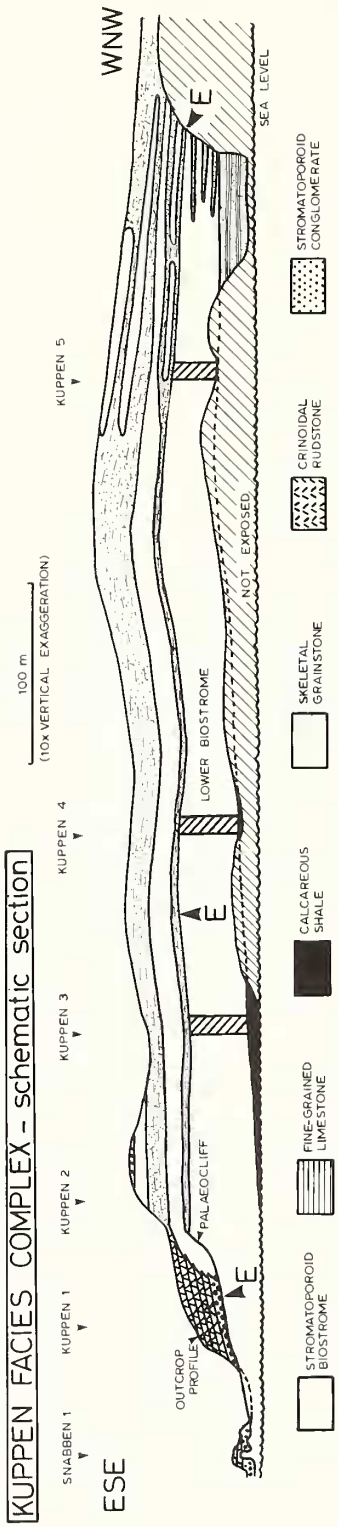
THE KUPPEN FACIES COMPLEX

The complex consists of several biostromes interbedded with argillaceous limestones, stromatoporoid conglomerates and crinoidal grainstones (text-fig. 2); the lowest biostrome is studied here. Stromatoporoid biostromes crop out in neighbouring areas, but only those at Kuppen were examined. Riding (1981, p. 65) recognized the biostromes as distinct from other organic build-ups on Gotland and applied the term 'Kuppen reef type'. He provided a log of the vertical facies changes at locality Kuppen 2 (see text-fig. 2), and noted lateral variations in the complex. Text-fig. 3 illustrates important selected features of the facies and displays the general character of the stromatoporoid morphologies.

As shown in text-fig. 2, the sequence begins with a poorly exposed argillaceous limestone containing a sparse stromatoporoid fauna. The overlying biostrome (from which the sample was collected) has, in most places, a crinoidal limestone basal bed, 30–50 cm thick, with stromatoporoid debris and some large stromatoporoids *in situ*. Pressure solution has extensively affected the stromatoporoids in places, such that in many the original morphology is unrecognizable. Biostrome sediment is most micritic fill between stromatoporoids, with lesser amounts of bioclastic material. The biostrome varies in thickness from 2·5 – 4 m and is everywhere terminated by an erosion surface, much of which is prominent and planar (text-fig. 3A and C; Munthe 1910, fig. 28); stromatoporoids are truncated, indicating that they were cemented into the matrix prior to erosion. An indeterminate amount of the upper section of the biostrome has been removed, and the erosion surface becomes more irregular towards the ESE, (text-fig. 3A). Minor sea level fluctuations could account for the vertical facies changes. The sequence is similar to the model provided by James (1984, p. 220) of shallowing-upwards carbonate units and to the example studied by Wilson (1967) in Devonian limestones of the Williston Basin of N. Dakota. Gypsum crystals in the upper part of the biostrome suggest the possibility of hypersaline conditions during a stage in the development of the biostrome (Kershaw 1987*a*), but no corroborative sedimentological evidence exists due to erosion of the top of the biostrome.

Dipping beds at Kuppen 1 are attributed to deposition on a slope associated with the palaeocliff (text-fig. 2), while undulation of bedding in the remainder of the complex is probably due to settling of the sediments on the shale at the base of the complex. There is only a slight tectonic dip across Gotland and the complex evidently formed on an approximately flat-lying sea bed. Lack of siliciclastics suggests a low hinterland, and consequently little terrigenous sediment transport into the area during the development of the complex. The SE area contains coarse skeletal limestones, whereas the NW areas with thin, interbedded, finer-grained limestone facies were quieter.

The current energy affecting the complex clearly varied. Most tall domical stromatoporoids are now on their sides, indicating that energy was relatively low to moderate while they were alive, but periodically sufficient to topple them. Substantial amounts of stromatoporoid debris also indicate higher energy events. The biostrome has the appearance of a mixed fauna (text-fig. 3), with many large stromatoporoids not disturbed from growth position, while debris was piled around them. Further thin biostromes interleaved with bedded limestones overlie the lower biostrome (text-fig. 2), but were not studied in detail. However, there are some differences in fauna; for example, the



TEXT-FIG. 2. Schematic section through the Kuppen facies complex showing vertical and lateral facies distribution dominated by stromatoporoid biostromes. Note the undulating erosion surface (E) truncating the top of the lower biostrome, with irregularities at the southern end of the outcrop, where small penecontemporaneously eroded stacks are present at Snabben 1. Here the biostrome is overlain by stromatoporoid conglomerate and crinoidal grainstones. Elsewhere, it is succeeded by interbedded biostromes and skeletal limestones. The lower biostrome thins to the WNW and is interrupted by skeletal grainstone beds. Hatched areas are sampling sites for stromatoporoids. Vertical exaggeration 10 ×.

biostrome overlying that studied here has a greater abundance of tabulate corals, particularly favositids.

Diagenesis

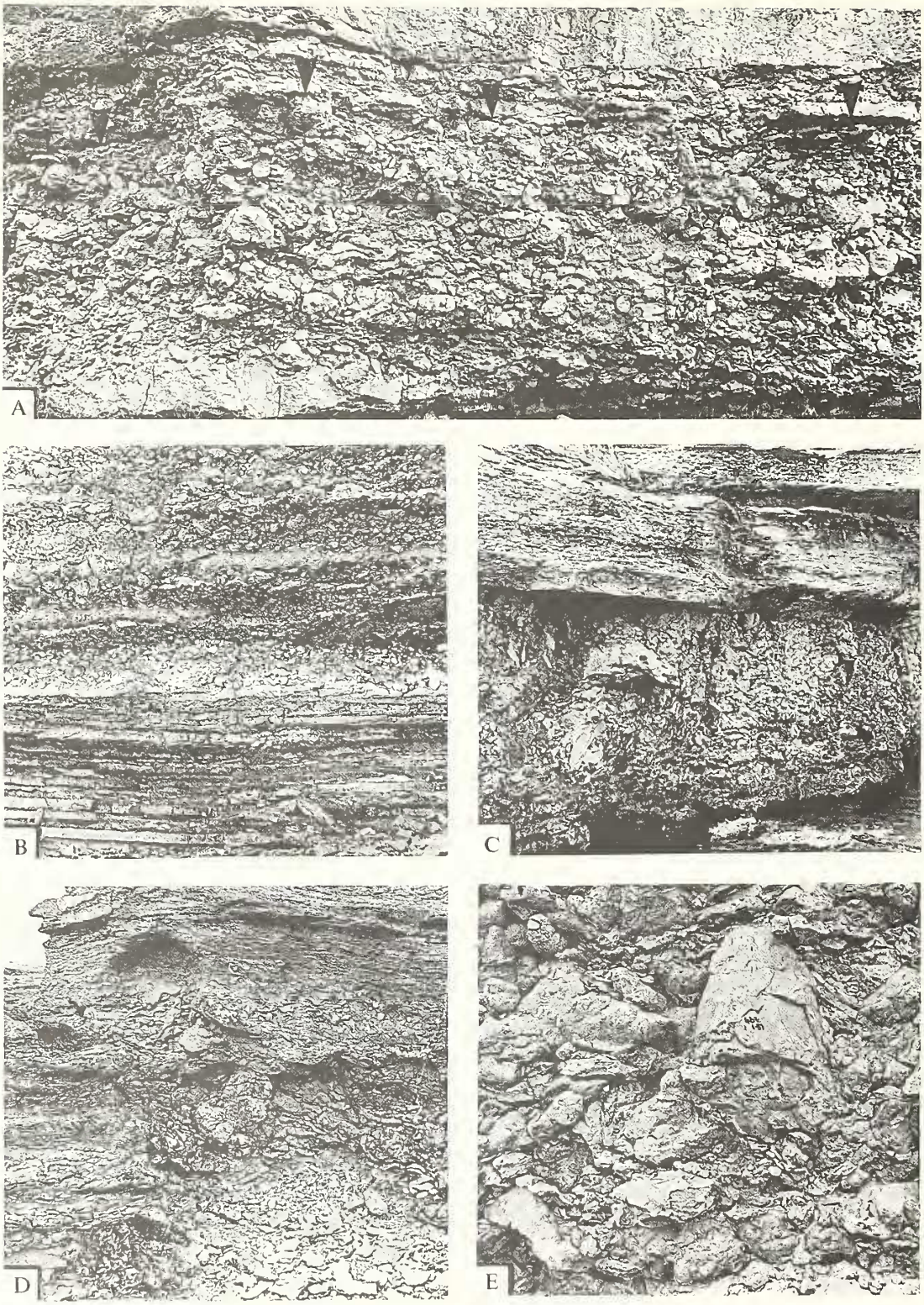
A full description of diagenesis of the biostrome is inappropriate here, but some aspects pertain to a taphonomic assessment of the stromatoporoids, so an outline of the important events is given. Three cement stages are recognized in both bioclastic fill and stromatoporoid galleries (text-fig. 4).

First stage cement forms non-luminescent (under cathodoluminescence – CL), non-ferroan syntaxial calcite on pelmatozoan debris. It is also present sporadically in stromatoporoid skeletal galleries (text-fig. 4B, D) and is most likely to be meteoric cement formed during uplift. Syntaxial cement on pelmatozoans is commonly regarded as meteoric because high Mg levels in sea water prevent its growth there; meteoric water is low in Mg. In the present sample, such cement fills most of the pore space of pelmatozoan grainstones, and leaves little doubt that it is of meteoric origin. There was apparently little marine cement, and this is corroborated by the common occurrence of toppled tall stromatoporoids. As noted by Kershaw (1981) some were toppled during life and show reorientated growth directions.

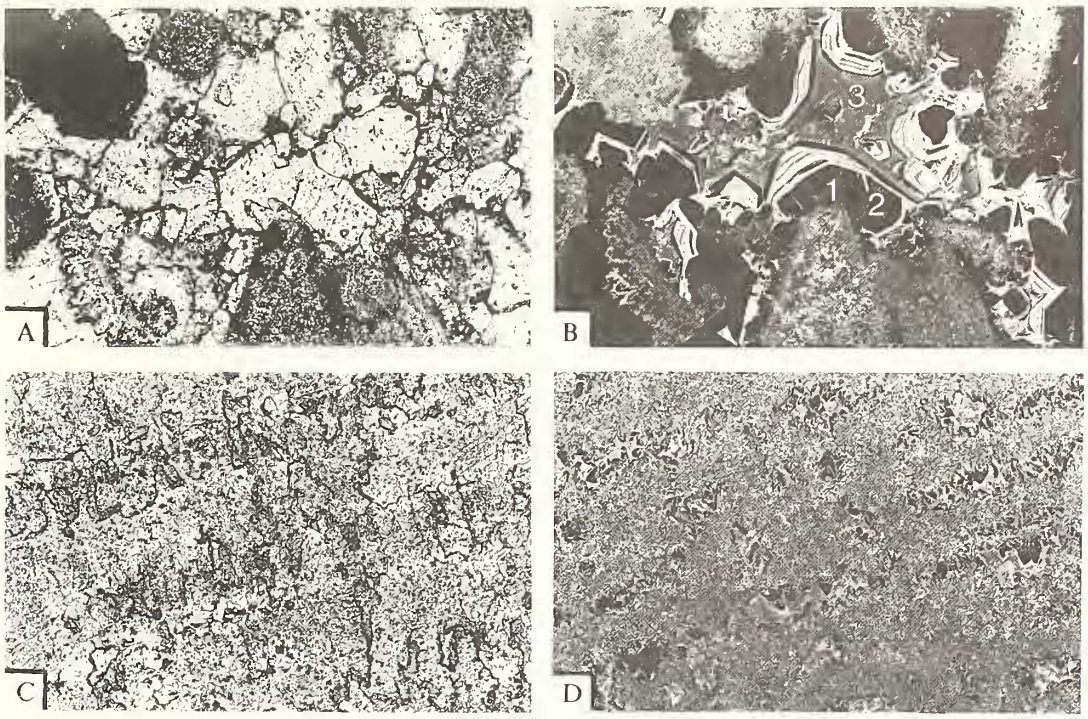
Second stage cement comprises very thin alternating bright and non-luminescent bands suggestive of subsequent burial near the redox boundary, with cyclic recharge of oxygenated water, a common situation in limestones (Scoffin 1987, p. 129). Staining of the same thin sections that were used for CL examination shows that these areas of the sections are also non-ferroan, which is consistent with the interpretation of such banded cement (under CL) being generated by the presence (bright) and absence (dark) of manganese, but with no iron present. The absence of iron is usually regarded as being due to its combination with sulphides liberated by action of sulphate-reducing processes on porewater sulphates in shallow burial, so that it is unavailable for inclusion into calcite lattices (Scoffin 1987, p. 129). This cement is again best developed in the porous pelmatozoan grainstone deposits and to a lesser extent in stromatoporoid skeletal galleries.

The final cement is dull luminescent and ferroan, where iron, now incorporated into the calcite cement following depletion of sulphides in pore waters, partially counteracts the bright CL effect of manganese (referred to as quenching). This cement, which probably indicates deeper burial, occupies the small remaining pore space in grainstones. However, most of the pore space of stromatoporoid galleries is usually filled with dull luminescent, ferroan cement, suggesting that it grew slowly at depth, after the biostrome had been buried. Since they represent largely closed porosity, stromatoporoid galleries are likely to have been less accessible to earlier pore waters. Comparable luminescent zones were observed by Dorobek (1987) in late Silurian – early Devonian carbonates in the Appalachians.

Stromatoporoid skeletons show a similar CL response to the pelmatozoan debris in the biostrome (text-fig. 4B, D). Also, all stromatoporoids in the assemblage are partially recrystallized. General observations by myself and other authors (Stearn, pers. comm. 1988; Watts 1981; Wood 1987) indicate that many stromatoporoids did not recrystallize as completely as aragonitic shells of molluscs, yet are consistently more recrystallized than the low Mg calcite of brachiopods. The inference that these stromatoporoids were therefore high Mg calcite originally is supported by a) the similarity of response in CL to pelmatozoans (high Mg calcite) and b) the widespread occurrence of microdolomite rhombs in stromatoporoid skeletons at Kuppen. Lohmann and Meyers (1977) discussed a burial diagenetic process whereby Mg expelled from high Mg calcite skeletons form localized dolomite. CL response and dolomite occurrence may of course be due to other diagenetic processes, but the partial recrystallization widespread amongst Silurian and Devonian stromatoporoids argues against low Mg calcite or aragonite original compositions. There is a wider issue of variation of stromatoporoid skeletal mineralogy through geological time and in relation to taxonomy, which requires investigation.



TEXT-FIG. 3. For legend see opposite.



TEXT-FIG. 4. Thin section views of typical material from the lower biostrome. A. Plane polarized light view of crinoidal grainstone from Kuppen 3A. B. Cathodoluminescence response of the same area, showing three zones of cement growth: 1. non-luminescent syntaxial cement on crinoids; 2. alternating bright and non-luminescent cements; 3. dull cement. Note the bright, dull and dark-speckled appearance of the crinoid fragments. C. Plane polarized light view of recrystallized stromatoporoid skeletal material of *Stromatopora venukovi* with crystal boundaries of neomorphic cement cutting across the stromatoporoid structure. The preserved laminae and pillar structure are difficult to recognize at this magnification, but galleries are discernible as sparry patches. D. Cathodoluminescence response of the same area shows the three cement zones in the galleries, plus a speckled luminescent character of bright, dull, and dark areas in the stromatoporoid skeleton. See text for discussion. All photos × 35.

FOSSIL ASSEMBLAGE OF THE LOWER BIOSTROME

Three accessible localities selected for intensive sampling are Kuppen 3, 4 and 5 (text-figs. 1 and 2), where the biostrome is 3·4, 3 and 2·5 m thick, respectively.

At each locality a grid was drawn on the vertical cliff face, 10 m long and of variable height depending on the thickness of the biostrome at that place. Each was divided into three parts parallel

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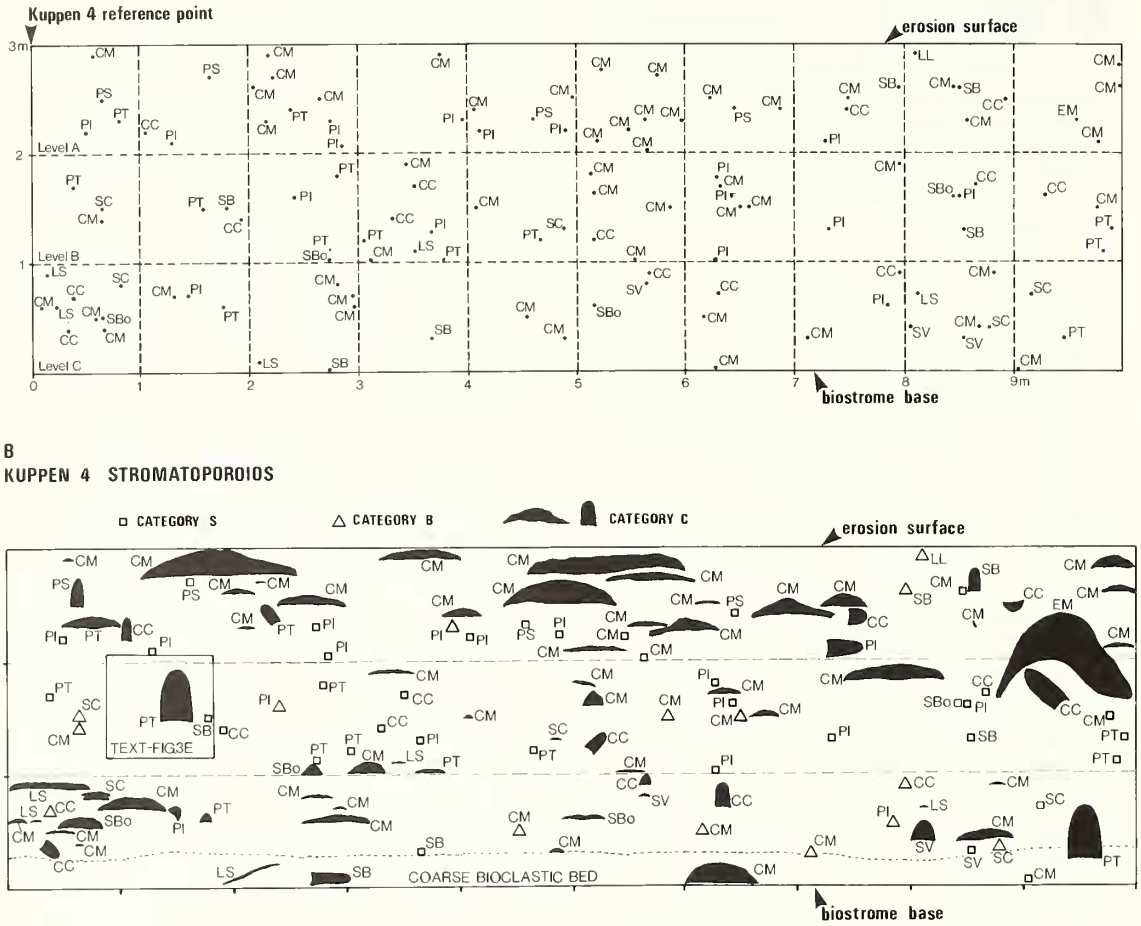
TEXT-FIG. 3. Photographs of selected parts of the Kuppen biostrome. A. Cliff face at Kuppen 5 showing basal bioclastic bed and densely packed stromatoporoids in the biostrome; length of view 8 m. B. Interbedded shales and limestones overlain by thin biostromes and limestone bands at the northwestern end of Kuppen; length of view 3·5 m. C. Biostrome at Kuppen 1, undercut by the sea where shale underlies the biostrome, and sharp erosion surface overlain by crinoidal gravel. Note the large, low domical stromatoporoid centre left in biostrome; length of view 5 m. D. Eroded stack (top left in hollow) at the biostrome top at Snabben 1, surrounded by stromatoporoid conglomerate and crinoidal gravel; length of view 3 m. E. Vertical section of central part of biostrome at Kuppen 4 (see text-fig. 5), showing laminar, low to high domical, broken and stylolitized stromatoporoids; length of view 0·95 m.



TEXT-FIG. 5. Schematic vertical section of the lower biostrome at Kuppen 4 to demonstrate sampling method. A. Sample locations of identified species, determined by vertical and lateral coordinates derived from random number tables. B. Morphology of the stromatoporoids sampled, illustrated in their preserved attitudes and positions. Three categories of preservation of growth form are recognized: *c* = complete specimens; *b* = broken skeletons, including small fragments; *s* = specimens so badly affected by pressure solution (stylolites) to make impossible any distinction between originally complete or broken. Specimens not identified are omitted from the diagram. Text-fig. 3E (inset) shows the general character of the outcrop. Stromatoporoid species are abbreviated in this and other diagrams, as follows. LL = *Labechia lepida*. CC = *Clathrodictyon convictum*, CM = *C. molticanum*, EM = *Ecclimadictyon macrotuberculatum*, PK = *Plexodictyon katriense*, DY = *Diplostroma yavorskyi*, PS = *Plectostroma scaniense*, PI = *P. intermedium*, SB = *Stromatopora bekkeri*, SC = *S. carteri*, SL = *S. lamellosa*, SV = *S. venukovi*, SBo = *Syringostromella borealis*, PT = *Parallelostroma typicum*, LS = *Lophiostroma schmidti*.

to bedding, here termed levels, of approximately equal thickness and labelled A, B, C, respectively from top to bottom (text-fig. 5). Bedding planes do not exist within the biostrome and so the level boundaries are artificial. Therefore levels are not necessarily time equivalent between localities.

Within each level, stromatoporoids were collected using random number tables to determine the precise collecting point and to obtain a representative sample of the assemblage (text-fig. 5). The

intention to collect 50 samples from each level at every locality was not possible and the final sample consisted of 404 specimens. Kuppen 5A was the worst affected with only 18 pieces retrieved. Of the total, 60 were unidentifiable, but these were evenly spread across sample sites (average of five in each) except in the case of Kuppen 3B, where 13 of 48 collected could not be classified. Thus the overall distribution of identified stromatoporoids is not unduly affected by the presence of unidentified samples. Almost all samples collected are stromatoporoids, with few corals. Heliolitids, however, are common in places, whereas favositids are rare. Kershaw (1987*b*) showed that 10% of stromatoporoids in this biostrome contain symbiotic corals; further samples revealed that in fact 20% of the stromatoporoid assemblage contains a variety of rugose corals and syringoporids, although this is unevenly distributed within the biostrome. Various other taxa, particularly echinoderms, are present as debris.

Since collecting was random, the data set provides a representative sample of the assemblage, and allows comparison within and between localities to furnish information on vertical and horizontal variation.

Stromatoporoid assemblage

Sixteen species distributed amongst several orders of stromatoporoids were found. Taxonomic revision by Stearn (1980) produces differences from the scheme applied by Mori (1969, 1970) to Gotland stromatoporoids which was used also by Kershaw (1981). Stearn's division into several orders is adopted here, giving the following list for the biostrome:

Order Lophiostromatida: *Lophiostroma schmidti* (Nicholson)
Order Labechiida: *Labechia lepida* Mori
Order Actinostromatida: *Plectostroma scaniense* Mori, *P. intermedium* Nestor, *Pseudolabechia granulata* Yabe and Sugiyama
Order Clathrodictyida: *Clathrodictyon mohicanum* Nestor, *C. convictum* Yavorsky, *Ecclimadictyon macrotuberculatum* (Riabinin), *Plexodictyon katriense* Nestor, *Diplostroma yavorskyi* Nestor
Order Stromatoporida: *Stromatopora bekkeri* Nestor, *S. carteri* Nicholson, *S. lamellosa* Yavorsky, *S. venukovi* Yavorsky, *Syringostromella borealis* (Nicholson), *Parallelostroma typicum* (Rosen).

These species are all well-known Palaeozoic forms and since they are fully described by Nestor (1966), Mori (1969, 1970), Stock (1979) and Stock and Holmes (1986), there is no need to illustrate them here. However, worth noting is that stromatoporoid classification is based on microscopic characters of laminae and pillar structure and arrangement. Two thin sections (vertical and horizontal) are required per specimen. The shape of the entire skeleton is not a diagnostic character, although some species are limited to certain shapes. Most species in the present sample are distinctive, but some raise taxonomic problems that are briefly discussed below.

Most specimens of *Stromatopora bekkeri* and *Parallelostroma typicum* are distinct, but some show such variability of structure of skeletal elements that occasional difficulty was faced in deciding into which species they should be grouped. Fagerstrom and Saxena (1973) recognized that variations of stromatoporoid structure within single thin sections can be high, but all within a single distinct species. Stock (1979), Stock and Holmes (1986) distinguished several species of *Parallelostroma* in the Upper Silurian of eastern America, with minor, but consistent, differences in skeletal structure defining the species. This is not possible in the present specimens, where variation, often in different parts of the same thin section, produces laminae and pillar arrangements resembling both species. The taxonomic uncertainty generated by these observations means that the distinction between these two species is unreliable. The possibility that they represent phenotypic variants of a single species cannot be discounted, although they could represent two species with overlapping skeletal morphology, clearly causing havoc with the morphospecies concept as applied to these species. The validity of other species at Kuppen is not questioned since they show consistent differences of skeletal structure. For the present purposes, *P. typicum* and *S. bekkeri* have been distinguished as separate species in text-figs. 5, 6, 8, 9 and 10, and the uncertain examples omitted, pending a separate analysis of this problem.

TABLE 1. Distribution of numbers of specimens of all identified stromatoporoids from Kuppen, arranged according to locality and level, with the three categories of *c* (complete), *b* (broken) and *s* (badly affected by pressure solution) indicated.

	Kuppen 3									Kuppen 4									Kuppen 5											
	Level A			Level B			Level C			Level A			Level B			Level C			Level A			Level B			Level C			Total		
Species	*c*	*b*	*s*	*c*	*b*	*s*	*c*	*b*	*s*	*c*	*b*	*s*	*c*	*b*	*s*	*c*	*b*	*s*	*c*	*b*	*s*	*c*	*b*	*s*	*c*	*b*	*s*	*c*	*b*	*s*
L. schmidti	—	—	—	—	—	—	4	—	1	—	—	—	1	—	—	4	—	—	—	—	—	1	—	—	5	—	—	15	—	1
P. typicum	—	—	—	1	1	—	—	—	—	2	—	—	2	—	7	2	—	—	—	—	—	2	—	3	2	—	2	11	1	12
S. borealis	6	1	—	1	—	1	1	—	—	—	—	—	1	—	1	2	—	—	—	—	—	—	—	—	—	—	—	11	1	2
S. venukovi	—	—	—	—	—	—	3	—	1	—	—	—	—	—	—	2	—	1	—	—	—	—	—	—	1	2	—	6	2	2
S. lamellosa	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—
S. carteri	1	—	—	—	1	1	1	—	—	—	—	—	1	1	—	1	1	1	—	—	—	—	—	—	—	—	—	4	3	2
S. bekkeri	1	1	—	4	3	—	8	3	1	1	1	—	—	—	2	1	—	1	—	—	—	4	1	2	3	—	1	22	9	7
P. granulata	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1	—
P. intermedium	2	13	4	—	1	—	1	1	—	1	1	6	—	1	6	1	1	—	5	—	4	8	—	5	2	—	6	20	18	31
P. scaniense	—	2	—	—	—	—	1	—	—	1	—	3	—	—	—	—	—	—	—	—	1	2	—	—	—	—	—	4	2	4
D. yavorskyi	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—
P. katriense	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	1	—	1
E. macrotuberculatum	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—
C. mohicanum	6	—	—	14	1	—	13	1	1	21	—	3	9	3	1	11	3	1	—	—	—	7	—	1	8	1	2	89	9	9
C. convictum	—	—	—	—	—	—	—	—	—	3	—	—	2	—	4	3	2	—	2	—	1	3	—	3	5	—	3	18	2	11
L. lepida	2	—	—	4	—	1	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	6	1	2

Plectostroma scaniense is distinguished from *P. intermedium* only by possessing astrorhizae (Nestor 1966, pl. XI; Mori 1970, pl. X). Many authors have discussed the taxonomic significance of these structures, and there is disagreement about their importance (see Stearn 1980, Wood 1987 for reviews). Both species exhibit the same growth form characteristics. I would accept that they could be the same species, but have left them separate in case future work should show them to be distinct.

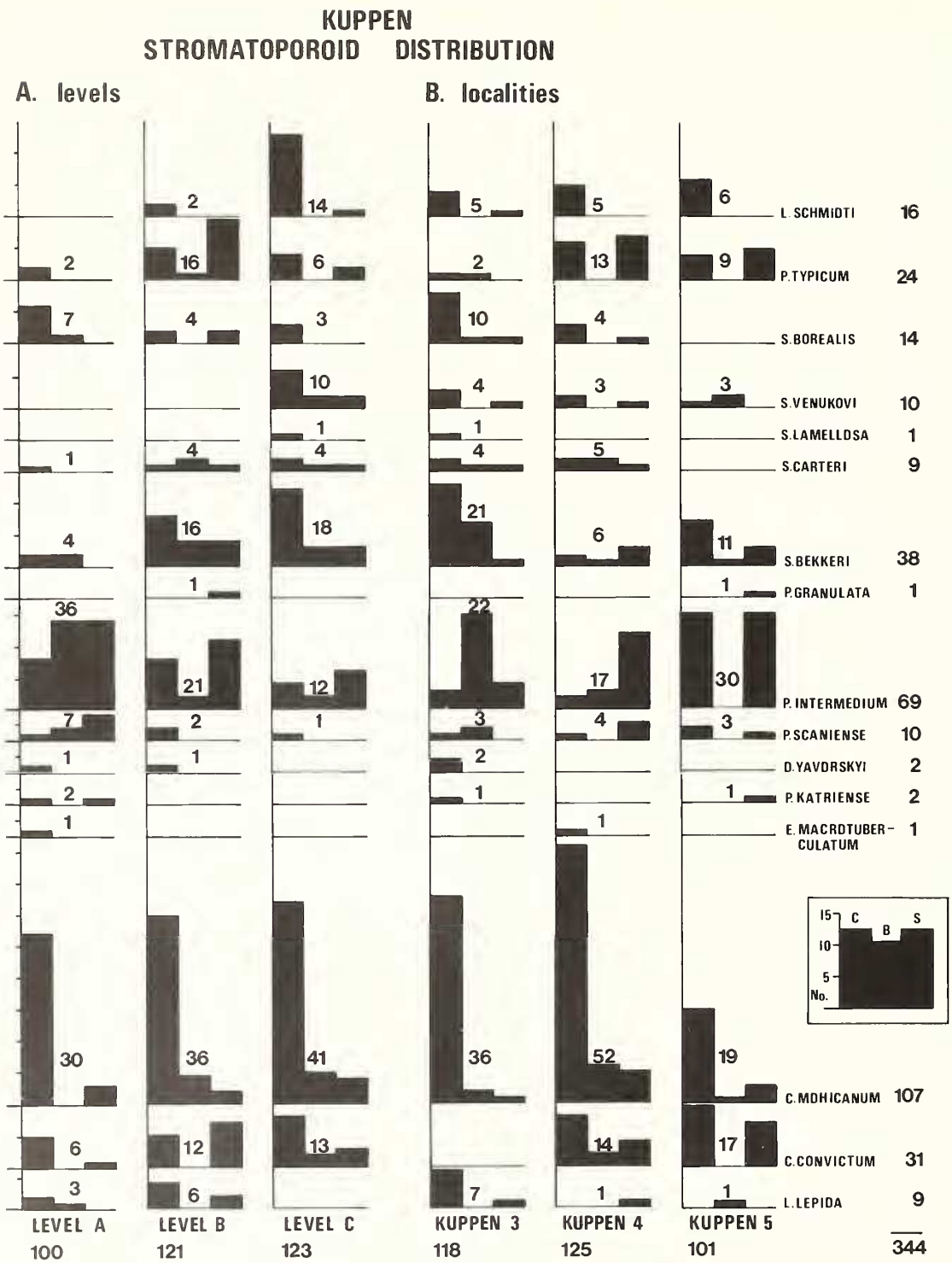
Stromatoporoid growth form

Table 1 shows the total identified sample, in each locality. Text-fig. 6 and Table 2 summarize the data into localities and levels for visual comparison. Division into three categories of preservation of the growth form (c, b, s; see Table 1) is important for morphological analysis. The most useful for morphological study are complete specimens (category c). Fragmented specimens (category b) are useful for studying biostratinomy, and specimens affected so badly by pressure solution that their shape cannot be determined (category s), were included to provide full information on specific distribution. Pressure solution effects are more pronounced at Kuppen 5 than at the more southerly localities. Dimensions of broken and stylolitized specimens were not recorded in the field; both are generally small, of the order of 10 cm in size, although larger specimens occur.

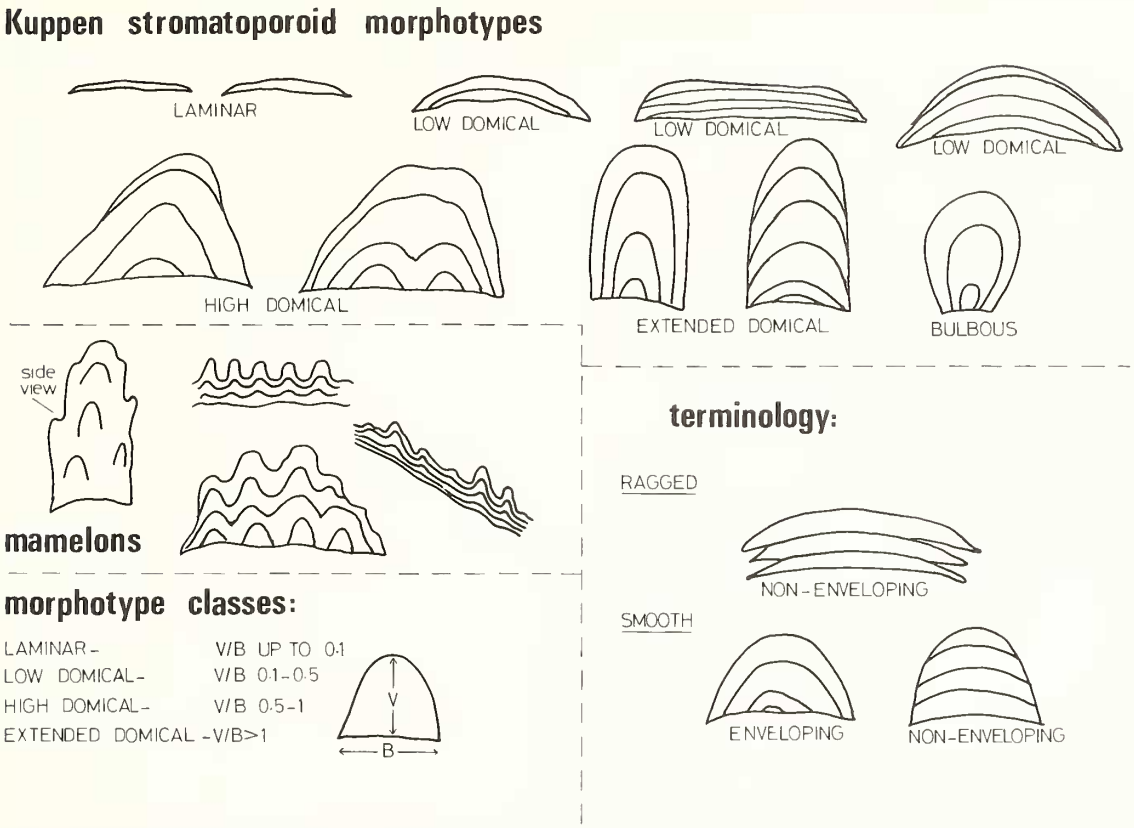
Growth forms fall into a relatively simple range from laminar to extended domical and bulbous of Kershaw and Riding (1978, 1980), illustrated in text-fig. 7. Most stromatoporoids have smooth outlines and rarely show ragged edges (where sediment periodically covered the flanks of skeletons). Within smooth outlines, laminae show different growth patterns. Some are completely *enveloping*, in which successive laminae cover all earlier laminae; others are *non-enveloping*, where growth produced additions at the apex and extended only a short distance down the flanks. Others have a combination of the two, and in these, lower stages of growth were enveloping while later growth was

TABLE 2. Distribution of numbers and percentages of complete specimens at Kuppen; note the large decrease of *Clathrodictyon mohicanum*, and increase of *Plectostroma intermedium* from Kuppen 4 to 5.

	Numbers of complete specimens							
	Kuppen 3		Kuppen 4		Kuppen 5		Total	
Species	No.	%	No.	%	No.	%	No.	%
L. schmidti	4	5·1	5	6·8	6	10	15	7·1
P. typicum	1	1·3	6	8·2	4	6·7	11	5·2
S. borealis	8	10·3	3	4·1	—		11	5·2
S. venukovi	3	3·8	2	2·7	1	1·7	6	2·8
S. lamellosa	1	1·3	—		—		1	0·5
S. carteri	2	2·6	2	2·7	—		4	1·9
S. bekkeri	13	16·7	2	2·7	7	11·6	22	10·4
P. granulata	—		—		—		—	
P. intermedium	3	3·8	2	2·7	15	25	20	9·5
P. scaniense	1	1·3	1	1·4	2	3·3	4	1·9
D. yavorskyi	2	2·6	—		—		2	0·9
P. katriense	1	1·3	—		—		1	0·5
E. macrotuberculatum	—		1	1·4	—		1	0·5
C. mohicanum	33	42·2	41	56·3	15	25	89	42·3
C. convictum	—		8	11	10	16·7	18	8·5
L. lepida	6	7·7	—		—		6	2·8
	78		73		60		211	



TEXT-FIG. 6. For legend see opposite.



TEXT-FIG. 7. Stromatoporoid morphotypes in the lower biostrome, showing a range from laminar to extended domical and bulbous, together with morphotype classification and terminology applied to the forms. These shapes are typical, simple, Silurian forms, shown in vertical section except where indicated. All growth forms can possess either enveloping or non-enveloping laminae. Very few are ragged and some show well developed mamelons.

non-enveloping. All three variations of smooth outlines are found in each of the more abundant species.

Attempts to quantify these features proved unrewarding; to determine the extent of enveloping and non-enveloping laminae in individual stromatoporoids requires medial vertical sections through skeletons. Only some specimens are suitably broken open in outcrop, and many individuals are displayed entire, obscuring the internal patterns. Therefore it has not been possible to determine the degree to which each style is developed at Kuppen, and graphical representations of morphology in the present study necessarily ignore these patterns in smooth stromatoporoids.

Because of the range of simple morphologies at Kuppen, the use of the parameterization scheme devised by Kershaw and Riding for graphically displaying stromatoporoid morphotypes is

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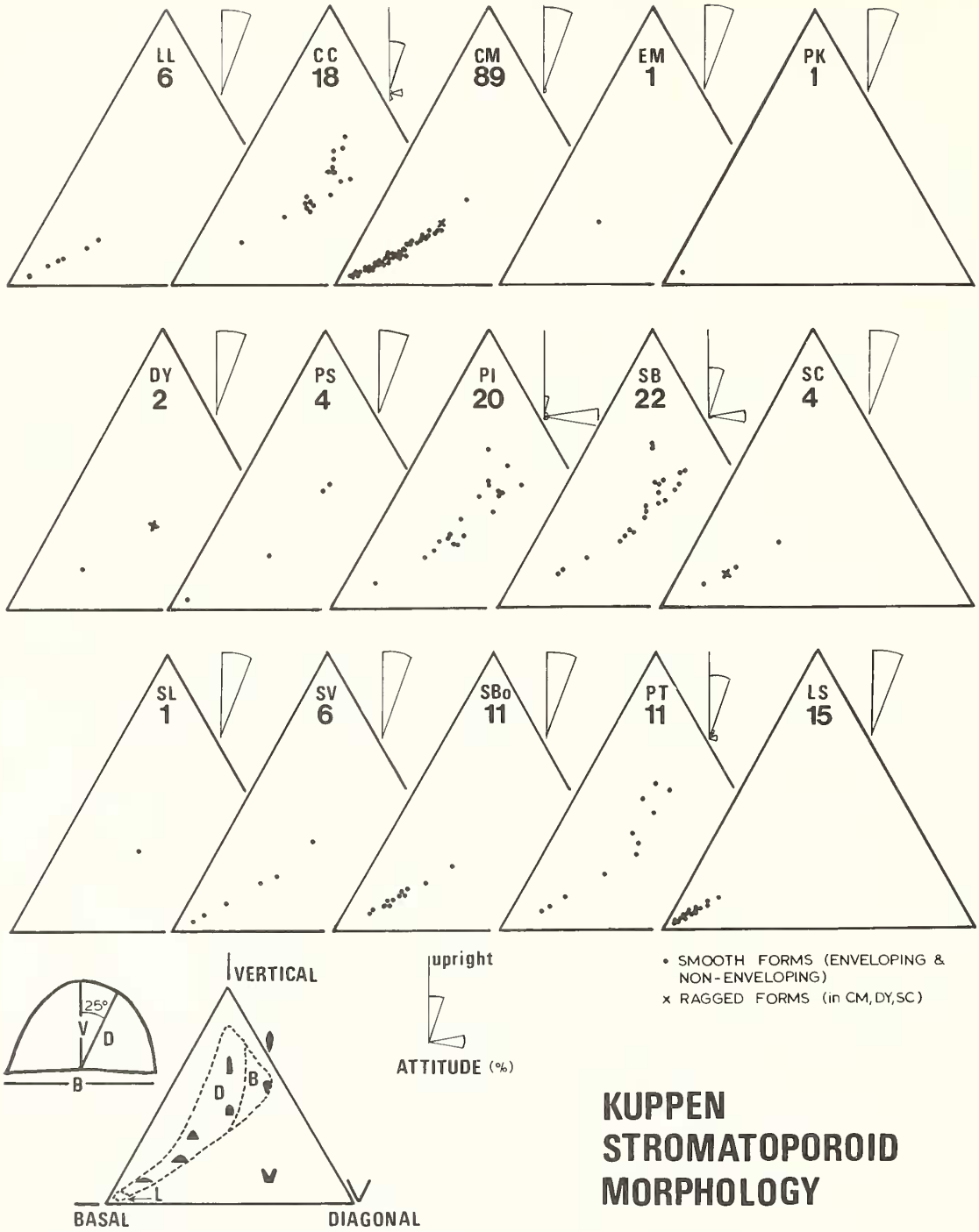
TEXT-FIG. 6. Graphical representation of the distribution of specimens of identified stromatoporoid species in the lower biostrome. The same data are arranged in two ways to illustrate vertical and horizontal variations. A. All specimens in each level. B. All specimens in each locality. Specimens are grouped into categories *c*, *b* and *s* according to the preservation of their growth form; see caption of text-fig. 5. Note abundance of *Clathrodictyon mohicanum*, and lesser amounts of *Plectostroma intermedium*, *Stromatopora bekkeri*, *Parallelostroma typicum*, *Clathrodictyon convictum*, *Syringostromella borealis* and *Lophiostroma schmidti*.



TEXT-FIG. 8. Triangular displays of morphology of all complete stromatoporoids in the lower biostrome, plotted using the Kershaw and Riding (1978) scheme. Morphology varies little between localities and levels in the biostrome, so species are illustrated grouped together. Inset shows measurements of basal diameter (B), vertical height (V) and diagonal length (D), and the morphological fields generated by the display. Partial rose diagrams of attitudes of skeletons are provided.

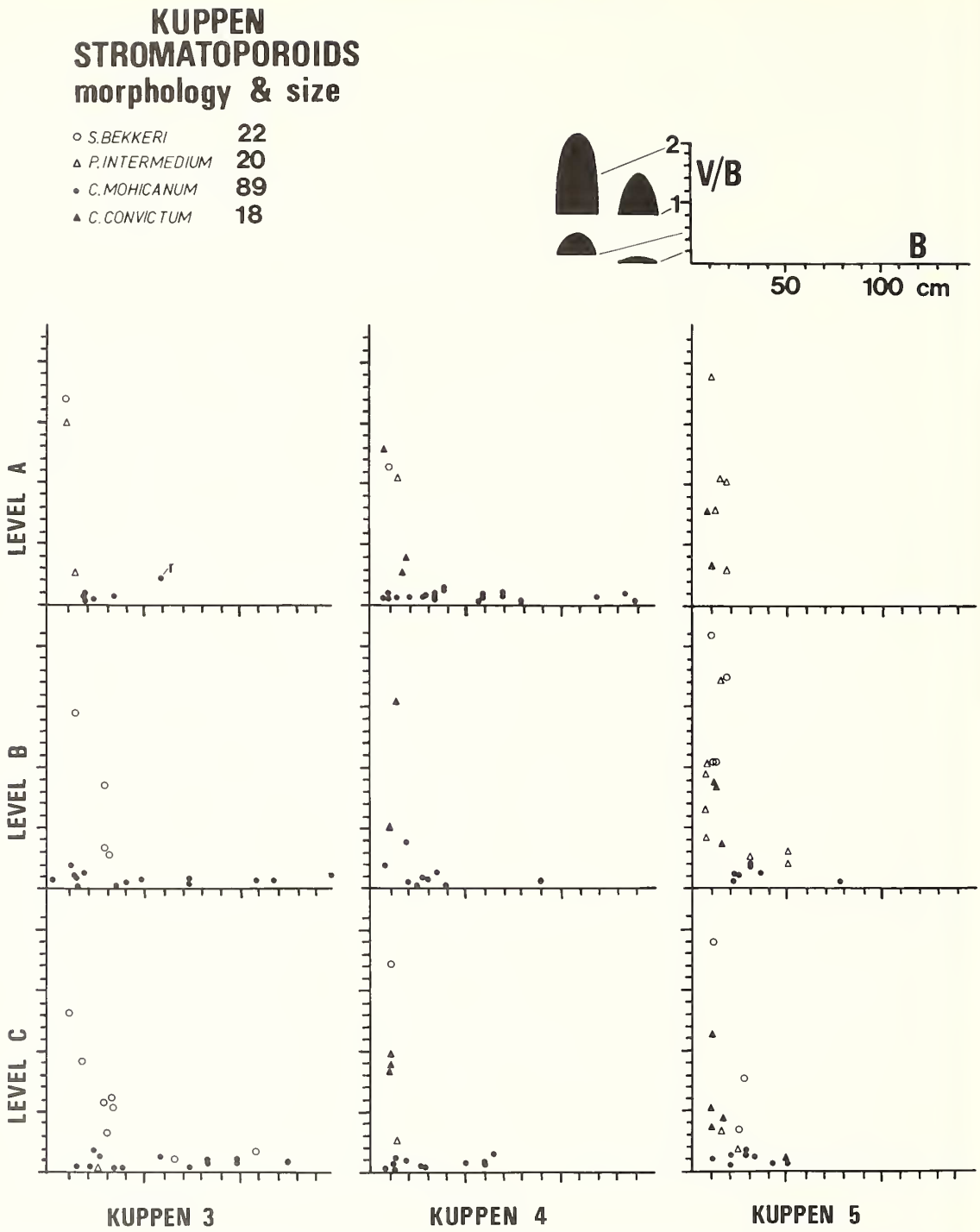
appropriate. Text-fig. 8 shows the plotted forms of all complete specimens; fragmented and stylolitized examples cannot be represented.

Text-fig. 8 shows that while many species, such as the ubiquitous *C. mohicanum*, are restricted to the lower profile fields, other species show a range of form from low to extended domical and bulbous. This suggests a phenotypic plasticity of the growth form of these species. *S. bekkeri* also seems not to be restricted to tall growth form as suggested by Kershaw (1981).

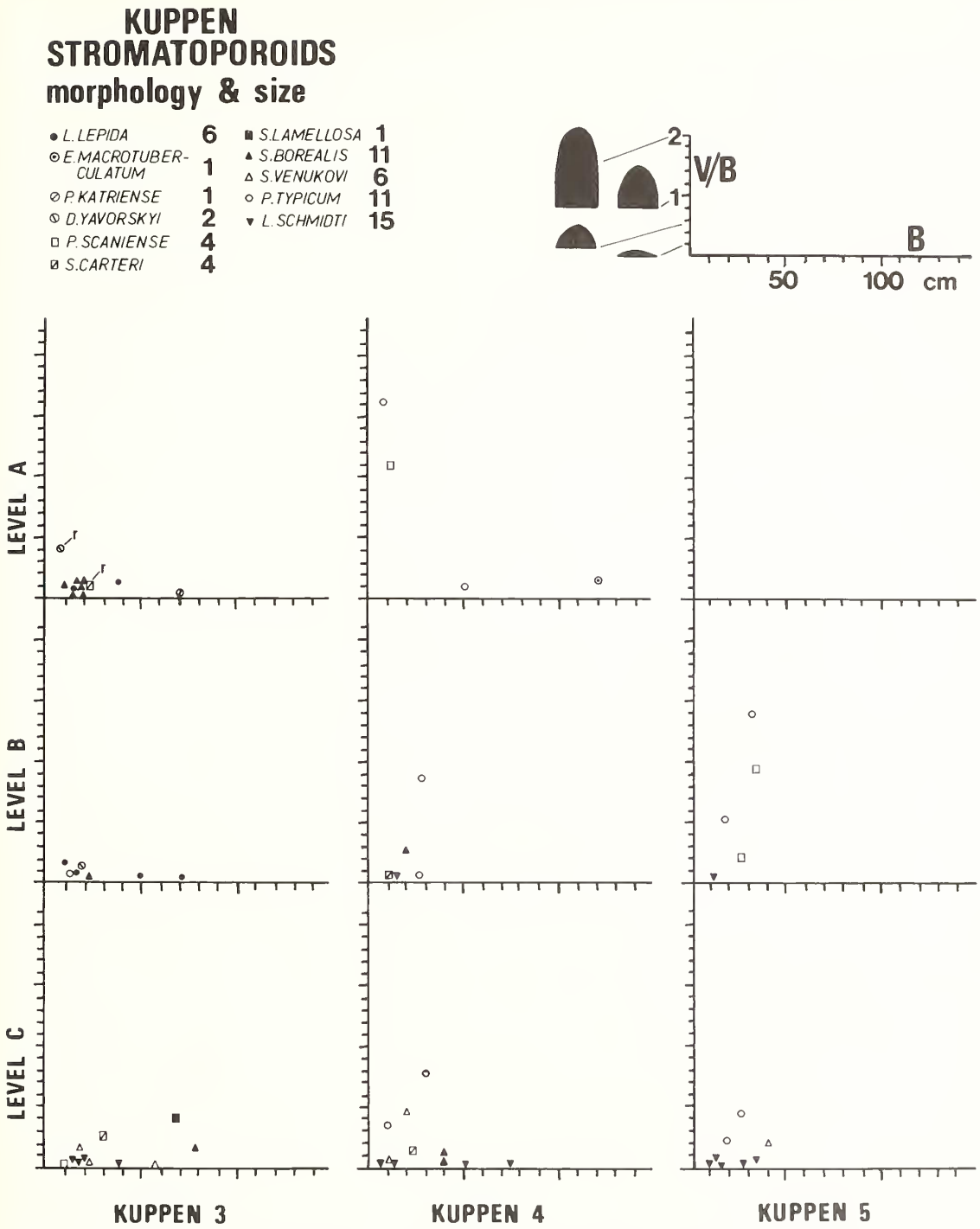
However, these displays take no account of the overall dimensions of skeletons. Since most growth forms plot on a line emanating from the basal corner, the most important components of the stromatoporoid morphology at Kuppen are B and V, with D having less effect. Therefore the V/B ratio in these specimens provides a crude measure of shape, and when plotted against B (text-figs. 9, 10), two clear trends are revealed in the more abundant species. For low profile forms, low B values are usually accompanied by low V/B ratios; but at higher B values, V/B stays low. For those species which can have taller forms, the graphs show that low B values are also accompanied by low V/B ratios, but at higher V/B ratios, B is still low (text-fig. 9). Furthermore, examination of early growth stages in the stromatoporoids shows those of tall forms to be low profile. Thus *Plectostroma intermedium*, *Clathrodictyon convictum Parallelostroma typicum* and *Stromatopora bekkeri* have a range of growth form from low to extended domical (text-fig. 9). Such ranges are present in most places sampled, and there is no evidence that they are restricted to low profile forms in particular sites on the biostrome. They are interpreted here as merely younger individuals. Therefore within these specimens, the early stages of growth are low domical, and the V/B ratio increased as the specimen grew, so that its morphology changed from lower to higher domical. Since ragged forms are rare at Kuppen, the taller morphologies are not an artifact generated by sedimentation, as can be the case in stromatoporoids in other environments. Graphs in text-fig. 9 consequently indicate that species adopted either lateral or vertical growth styles, giving low or high profile forms, respectively. These features are summarized in text-fig. 11.

Although the two-fold growth response pattern is clear, there is not as sharp a dichotomy of growth style as this discussion may imply. In text-figs. 9 and 10 a few specimens of *Clathrodictyon convictum*, *Parallelostroma typicum*, *Stromatopora bekkeri* and *Plectostroma intermedium* are large low profile stromatoporoids, which therefore do not fit the pattern. In the field, these stromatoporoids were shown to have more than one growth centre, so that these forms can be accounted for by coalescence of several specimens of one species which happened to grow near each other, and merged as they grew. Coalescence is common amongst conspecifics in stromatoporoids, so presumably there was no immune system response of individuals to members of the same species. Not all coalesced examples became large, low domical forms; cases of extended domical coalesced specimens were found at Kuppen, and the final growth form appears to have been controlled by the number and spatial distribution of conspecifics involved in its generation (text-fig. 11). The same process probably accounts for the larger specimens of *C. mohicanum*, but cannot be recognized satisfactorily in the field because laminae are usually undulose and identification of separate early growth stages is difficult.

Little information is available on morphologies of these stromatoporoids in other localities. Combining information from reports on Silurian stromatoporoids from elsewhere on Gotland, Estonia (Mori 1970; Nestor 1966), Canada (Savelle 1979) and New York (Stock 1979), it is clear that morphologies of *Labechia lepida*, *Clathrodictyon convictum*, *C. mohicanum*, *Stromatopora carteri*, *S. bekkeri*, *Lophiostroma schmidti*, and *Syringostromella borealis* are broadly similar to these species at Kuppen, but several species have also been found with other growth forms. *Ecclimadictyon macrotuberculatum* can be high domical and bulbous in addition to the low domical specimen at Kuppen; *Plexodictyon katriense* is laminar at Kuppen, but domical elsewhere; *Diplostroma yavorskyi* is extended domical as well as the low domical form found at Kuppen; *Plectostroma scaniense* and *Parallelostroma typicum* can be laminar as well as the domical forms at Kuppen. *Stromatopora venukovi* has been reported as domical elsewhere, but at Kuppen there are also laminar forms. These descriptions are not based on comprehensive data, but imply differences in response of these species in other environments.

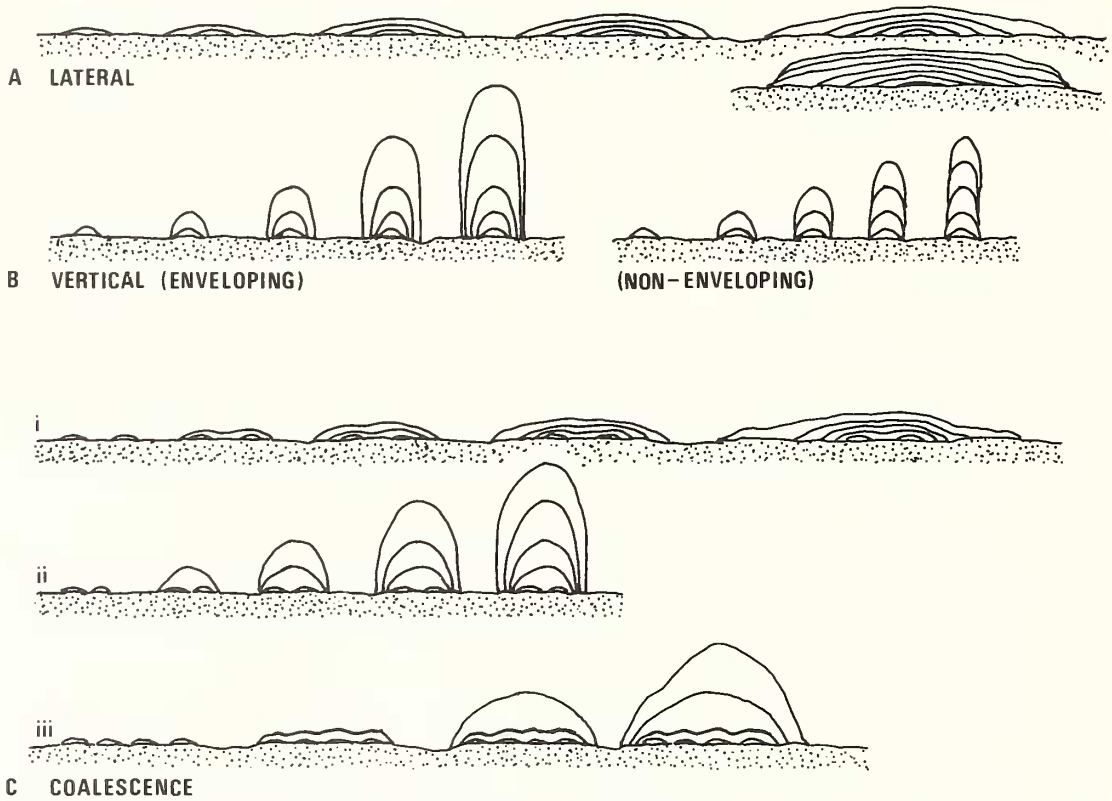


TEXT-FIG. 9. Graphical representation of stromatoporoid morphology, using V/B ratio in relation to basal diameter for the four most common species at Kuppen, arranged according to levels and localities to illustrate abundance and variation in size and morphology. Inset shows scales and morphologies represented by the graphs. Two distinct trends are present, vertical and lateral. See text for discussion.



TEXT-FIG. 10. Graphical representation of stromatoporoid morphology, using V/B ratio in relation to basal diameter for the less common species at Kuppen, to illustrate abundance and variation in size and morphology. Inset shows scales and morphologies represented by the graphs.

Kuppen stromatoporoid growth styles



TEXT-FIG. 11. Stromatoporoid growth styles in the lower biostrome, interpreted from text-fig. 9. A. lateral style, developed in low profile forms, such as *Clathrodictyon mohicanum*. B. Vertical style, formed by high profile forms, such as *Plectostroma intermedium*. Many develop enveloping laminae, but others are non-enveloping, while retaining the smooth outline. See text for discussion. C. Forms produced by coalescence of several specimens of the same species which grew near each other. (i) some large low domical forms may be due to this; (ii) high and extended domical forms may contain a small number of early growth stages; (iii) many specimens coalescing may mask the vertical growth style and produce large, low to high domical forms of species which would otherwise be extended domical. Some examples of *Stromatopora bekkeri* and *Plectostroma intermedium* in text-fig. 9 are due to this feature.

Morphology of *Plectostroma scaniense* and *Parallelostroma typicum* was examined in more detail by Mori (1970, figs, 23 and 28). His graphs of height plotted against diameter for specimens of these species, in several stratigraphic units on Gotland, reveal considerable variety of morphology and size. Using Mori's data, V/B was calculated, and plotted against B, as in text-figs. 9 and 10. The results are not presented here, but show that, in the Hemse Beds, both species have a range of form from laminar to high domical. Some low profile skeletons are large and may be due to coalescence, although this is not determinable from Mori's data. In the Sundre Beds (upper Ludlow), however, Mori's data show that almost all specimens of both species fall into the low domical field (V/B = 0·1 – 0·5), and some large forms are laminar, including a specimen of *Plectostroma scaniense* c. 70 cm in diameter (= B). Although Mori's graphs combine data from reef and non-reef localities, Mori (1970, p. 45) noted that stromatoporoid reefs in the Hamra and Sundre Beds are dominated

by low profile forms, and my own field examination revealed a remarkable lack of tall stromatoporoids. Therefore coalescence cannot be responsible for the low profiles, and there is clearly a lateral growth style in these specimens from the Sundre Beds.

STROMATOPOROID DISTRIBUTION AND BIOSTRATINOMY

Stromatoporoid morphology is not uniformly distributed in the biostrome. Visual examination along the length of the outcrop shows that large, low profile forms are most abundant between Snabben 1 and Kuppen 4, but from Kuppen 4 towards Herrvik Harbour such forms decrease in abundance and taller stromatoporoids are more common. Also, the number of stromatoporoids with symbiotic (in the broad sense of the term) syringoporids and rugosans dramatically increases just north of Kuppen 4, and in places is much greater than the 20% average for the biostrome quoted earlier. Sampling the entire length of the biostrome was impractical because of access to the cliff, but the sample sites chosen are clearly representative of the variations present. The only obvious vertical change in the biostrome is that the upper 0·5 m between Kuppen 2 and Kuppen 4 contains stromatoporoids commonly of smaller size, with a more rubbly general appearance than the lower portions.

Text-fig. 6 shows heterogeneity in the vertical and lateral abundance of several species in the biostrome, and analysis of this variation is important to determine palaeoecological characters of the stromatoporoids. The more abundant species show variations as follows. *Lophiostroma schmidti* and *Stromatopora vemukovi* are present only in the basal part of the biostrome, but in all localities; *Parallelostroma typicum* and *Stromatopora bekkeri* occur throughout (including Kuppen 2; Kershaw 1981) but rarely in the upper portion of the unit; *Syringostromella borealis* occurs only at Kuppen 3 and 4 with more specimens in the upper part; *Stromatopora carteri* also occurs only at Kuppen 3 and 4, but rarely in the upper part; *Plectostroma intermedium* is widespread throughout the biostrome with a lot of fragments at Kuppen 3, and was also found at Kuppen 2 (Kershaw 1981); *Clathrodictyon mohicanum* is abundant everywhere (including Kuppen 2: Kershaw 1981), but diminishes slightly at Kuppen 5; *C. convictum* is more abundant in the lower part, but is missing in Kuppen 3 (one specimen at Kuppen 2: Kershaw 1981); and lastly *Labechia lepida* is uncommon, but is missing from the lower level, and rare at Kuppen 5.

Most laminar to low domical stromatoporoids (e.g. *C. mohicanum*, *Lophiostroma schmidti* and *Syringostromella borealis*) are complete, upright and probably did not suffer much damage (effects of abrasion have not been recognized because of pressure solution on the stromatoporoid margins). Laminar to low domical forms of all species are usually upright, irrespective of basal diameter. All the species with these morphologies comprise a well developed calcite skeletal structure, with robust laminae and pillars, expected to provide considerable strength to their skeletons. Most of the higher profile species, including *Parallelostroma typicum*, *Stromatopora bekkeri* and *Clathrodictyon convictum*, are also complete, but are commonly overturned (text-fig. 8), and in some cases more damaged than stromatoporoids of lower domical shapes (text-fig. 6). *Plectostroma intermedium* suffered considerable damage in places.

The lack of open reef framework and early cementation permitted ready movement of debris across the biostrome, and this has clearly happened to a substantial number of stromatoporoid fragments. Comparisons of stromatoporoid abundance and growth form between localities can be usefully studied only using complete specimens. Distribution of fragments, however, provides information on severity of damage to stromatoporoids and is a necessary part of ecological study. Since fragments are generally small, around 10 cm across, a large number can be derived from a single stromatoporoid. However, assessment of the number of missing whole stromatoporoids represented by the fragmented material is unrealistic because of the variation in size of complete specimens and of the unknown degree of transport into, and out of, the Kuppen area. Nevertheless, in many species the degree of damage is small, especially in *Clathrodictyon mohicanum*, giving the impression that only a small number of these were broken up during high energy. In the case of *Plectostroma intermedium*, although no broken specimens were recorded in the sampling grid at

Kuppen 5, half the sample there is affected by pressure solution. Its effects distort the relative numbers of complete and broken samples, because most specimens in category s were of small dimensions, and are likely to be fragments; consequently damage to *P. intermedium* is most probably even greater than text-fig. 6 implies. The difference in damage between *C. mohicanum* and *P. intermedium* can be partly attributed to the more easily damaged taller form of the latter, but *P. intermedium* is the most damaged of all the stromatoporoids in the suite and especially so in the upper part of Kuppen 3. The skeleton of this species consists of a network of thin pillars and processes instead of the strong skeleton characteristic of other species with tall forms at Kuppen. Its skeleton appears delicate in thin section and, as has been shown earlier, the majority of cement filling stromatoporoid galleries is dull luminescent, suggesting late (burial) cement. Thus the observed degree of damage is consistent with interpretation of an easily damaged, brittle structure whilst on the sea bed. Consequently the growth forms and skeletal structures of the stromatoporoids possess different preservation potentials. Although most showed non-significant results when using chi-squared tests, comparisons between numbers of specimens of *P. intermedium* and *C. mohicanum* show clearly than the former is significantly more damaged at Kuppen 3 at the 5% level. Chi-squared tests between *P. intermedium* and combined numbers of *Parallelostroma typicum* and *Stromatopora bekkeri* showed the same result. This confirms the impression of a delicate structure to *Plectostroma intermedium* compared to the more robust skeletons of *Parallelostroma typicum*-*Stromatopora bekkeri*. All these species have similar morphologies (text-fig. 8).

Statistical comparisons are also instructive to assess the general character of the distribution of complete stromatoporoids. Statistical tests were used to compare stromatoporoids between localities, and between levels within localities, but not between levels combined from different localities since level boundaries are arbitrary and no reliable correlation can be made between them. Tests on the distribution of specimens, and of growth forms, show a variety of results. Chi-squared tests were used to compare numbers of complete specimens of pairs of species between localities to determine distributional relationships, and therefore lateral variation. Importantly, *Plectostroma intermedium* increased significantly from Kuppen 4 to Kuppen 5, and over the larger distance from Kuppen 3 to Kuppen 5 when compared with *C. mohicanum* (1% level). *C. convictum* increases significantly from Kuppen 3 to Kuppen 4 in contrast to *C. mohicanum*, and also from Kuppen 3 to Kuppen 5 when tested with *C. mohicanum* and *Syringostromella borealis* at the 5% level. Tests involving *Parallelostroma typicum* and *Stromatopora bekkeri* were considered unreliable in view of taxonomic problems and were omitted. Tests using other species were not particularly informative in view of the small numbers, although much variation in distribution is evident from Table 1 and text-fig. 6.

The above tests illustrate large scale lateral changes, but variations can be recognized between levels within localities. Thus each level is considered to be time-averaged and compared as a unit with other levels to illustrate temporal changes in the development of the stromatoporoids at any site. With use of the Fisher exact probability test, the visual decrease in basal diameter (a measure of size) of *C. mohicanum* from Kuppen 3B to 3A (text-fig. 9) is significant only at the 13% level, and the increase from 4B to 4A at the 9% level. With levels combined to compare localities, the visual reduction in size from Kuppen 4 to 5 reveals significance at the 11% level. These results are therefore not regarded as significantly different. The Fisher test also reveals a non-significant result when the V/B ratio (a measure of shape) in *Plectostroma intermedium* is compared between Kuppen 4 and 5 ($P = 0{\cdot}48$) and when Kuppen 5 is compared to both Kuppen 3 and 4 combined ($P = 0{\cdot}24$). Thus specimens of this species are not significantly taller at Kuppen 5 than at Kuppen 4 or Kuppen 3, as might be expected in the quieter environment of Kuppen 5.

To summarize important features of the tests: *C. mohicanum* (a low profile form) is significantly less abundant at Kuppen 5 compared with *Plectostroma intermedium* (a tall profile form), which increases sharply at Kuppen 5; *C. mohicanum* varies in size between levels and localities, but not significantly, and some less abundant species show fluctuations in abundance laterally in the biostrome. It can be argued that the striking difference in distribution of numbers of whole samples of *C. mohicanum* and *P. intermedium* is an artifact caused by extensive damage to *P. intermedium*

at Kuppen 3A. However, it should be noted that the number of whole specimens of *P. intermedium* which would need to have been destroyed to generate the fragments is relatively small, because debris is much smaller than whole specimens, even if the stylolitized samples (most of which were probably originally fragments) are included. Also, no fragments of *C. mohicanum* were collected from Kuppen 3A, and the complete specimens were of smaller size than in most other sites (text-fig. 9). Other species with a variety of growth profiles are represented largely by complete specimens in Kuppen 3A (Table 1), and the overall impression is of localized movement of debris. Variations in distribution of stromatoporoid species vertically and laterally throughout the biostrome support this (text-fig. 6 and Table 1) and reflect the life distribution of the stromatoporoids, thus broadly relating to their palaeobiology.

Lastly, a curious feature of the Kuppen stromatoporoids is a notable lack of bioerosion. Stromatoporoids from the Upper Visby Beds (lower Wenlock, Gotland), for example, are heavily bored by *Trypanites*, but not at Kuppen. Thus the damage to stromatoporoids at Kuppen can be safely attributed to physical processes.

CONTROLS ON STROMATOPOROID GROWTH

The very high abundance of stromatoporoids in the biostrome was an important aid to the development of its fauna, because of the provision by taphonomic processes of a substrate of dead skeletons of earlier individuals. Particularly significant is the dominance of low profile stromatoporoids. *C. mohicanum* must have acted as a key substrate stabilizer, and *Lophiostroma schmidti*, with its characteristic encrusting habit, would have assisted in immobilizing areas of substrate. Some specimens of this latter species are large (text-fig. 10), and occur in the lower portion of the biostrome as well as in the marl beneath. In the absence of a cemented frame, the stability of laminar and low domical stromatoporoids in a regime of low sedimentation, allowed repeated colonization of the surface. Encrusting crinoids, bryozoans, and rugose and tabulate corals have also made use of this facility. *L. schmidti* was also commonly found encrusting, and was encrusted by, other stromatoporoid species, a feature noted by Mori (1970).

Distributions of species in the lower biostrome are clearly heterogeneous. The south end of the Kuppen complex shows coarser grained sediments overlying the biostrome, and deep palaeo-erosion into it. The northwestern end (at Kuppen 5) shows a thinning of the unit and frequent interfingering of sediment in the area between Kuppen 5 and Herrvik. Lower energy water permitting a higher sedimentation rate in the Kuppen 5 area would have selected taller forms, and prejudiced survival of low profile stromatoporoids because of greater chance of them being buried. This could account for the distributional differences between *P. intermedium* and *C. mohicanum*, but paucity of ragged forms implies an overall low depositional rate. Most specimens of *Clathrodictyon convictum* show a smooth non-enveloping form, suited to a lower energy situation with an increased sedimentation rate at Kuppen 5, so that growth was concentrated at the apex of individual stromatoporoids. The small numbers and size of *C. mohicanum* at Kuppen 5 could be taken to indicate inhibition of growth by slow continuous sedimentation, rather than periodic deposition which would have led to development of ragged forms.

Species-morphology relationships in the Kuppen suite show a pronounced taxonomic control on growth form (text-figs. 8–10), and illustrate ontogenetic patterns in growth form development (text-fig. 11). The reasons why different species developed different growth forms, however, remain undiscovered. While sedimentation rate is invoked here to play a part in controlling distribution, the abundance of low profile forms and rarity of ragged shapes indicates an overall low rate of deposition for the biostrome, and therefore sedimentation cannot be inherently responsible for the differences in form. In conditions of low energy, some species may have grown upwards to create local turbulence as suggested by Kershaw (1981). This speculative point could be invoked to explain why tall forms grew in the NW area, but since high and low profile forms occur upright and in close proximity in the southern area at Kuppen 2 (Kershaw 1981) and can be satisfactorily regarded as being *in situ*, such an interpretation cannot be generally applied. Also, apart from those at the base

of the biostrome, there was no need for low profile forms to develop as a response to avoid sinking in soft sediment, because their substrate was mostly dead skeletons of stromatoporoids, suitable also for taller forms because of the stability of a hard surface.

Work on Devonian stromatoporoids illustrates the importance of lateral growth as a competitive feature (Meyer 1981), which would account for the abundance of *C. mohicanum*. However, competition for space between stromatoporoids at Kuppen, whereby fast growing, low profile forms would have commanded large areas of substrate, forcing others to grow upwards, cannot explain the dichotomy of form because of the different distributions of *Plectostroma intermedium* and *Clathrodicyon mohicanum* (text-fig. 6). Abundance of low profile shapes could be related to a competitive feature, but also to adaptation to an occasionally turbulent environment with storm action selectivity removing taller forms periodically. Since energy was lower most of the time, a low profile shape would only be necessary for that purpose in times of high energy.

Recent work on other stromatoporoid assemblages also indicates the selective advantage of lateral growth. Harrington (1987) describes the usefulness of a lateral growth habit for colonizing unstable substrates in Devonian stromatoporoids. Bjerstedt and Feldmann (1985) show how stromatoporoid morphology varies from stabilizing, low profile forms in the lower parts of a Middle Devonian reef to more erect shapes once stabilization has been achieved. Therefore the development of a low profile form can be explained in a number of ways, with difficulty in distinguishing between them. Thus at Kuppen the presence of higher profile forms could be attributed to fluctuations of environmental energy, allowing periodic colonization by stromatoporoids with high profile shapes which were selectively damaged during storms.

Stromatoporoids which normally formed tall shapes are occasionally large, low domical morphologies (text-fig. 9). These are demonstrably due to coalescence of several individuals, and the simultaneous growth of a number of stromatoporoids near each other is circumstantial evidence for growth on dead areas of substrate since closely packed fossils were not necessarily alive simultaneously. In the case of *Stromatopora bekkeri* (text-fig. 9), the location of these particular specimens at the base of the biostrome at Kuppen 3 is also notable, their substrate being the underlying bedded marls (text-fig. 2) poorly populated by stromatoporoids. Development of a low profile form in this situation would also help to spread weight on a soft substrate. Kershaw (1984) suggested substrate control for low profile forms in the Upper Visby Beds (Wenlock) on Gotland.

Data presented by Mori (1970), noted earlier, show that stromatoporoid reefs in the Sundre Beds are dominated by low profile stromatoporoids. This reinforces the importance of a low profile in reef-builders. The principal species in these Sundre reefs, *Plectostroma scaniense* and *Parallelostroma typicum*, are tall forms at Kuppen, while the dominant stromatoporoid at Kuppen, *Clathrodictyon mohicanum*, is missing from the Sundre Beds (upper Ludlow, younger than the Hemse Beds). There is clearly a need to investigate the reasons for these differences, which may involve environmental changes, selecting for some species and excluding others. However, the possibility of adaptive evolution towards a more efficient growth form in some species also needs to be considered.

Stromatoporoid growth irregularities

Some stromatoporoids at Kuppen exhibit small protrusions, called mamelons, 0·5 – 2 cm in height, and not associated with astrorhizae as mamelons sometimes are. They occur rarely in *Stromatopora bekkeri*, *Parallelostroma typicum*, *Plectostroma scaniense*, and *P. intermedium*, but they covered the upper surface of the skeleton in 7 of the 107 specimens of *C. mohicanum*. They were vertically orientated in specimens which lay with their basal dimension horizontally on the substrate, but one specimen lying at an angle of *c.* 30° from horizontal in the upper part of Kuppen 3 still had vertically orientated protrusions (text-fig. 7). This latter feature was also found in several unidentified stromatoporoids from other parts of the biostrome and a recrystallized stromatoporoid from a biostrome in the Klinteberg Beds at locality Vivungs 1 of Laufeld (1974*a*), and lead to speculation as to their cause.

Boyajian and La Barbera (1987) investigated mamelons experimentally in conjunction with astrorhizae in model stromatoporoids and *Ceratoporella nicholsoni* and showed their importance in

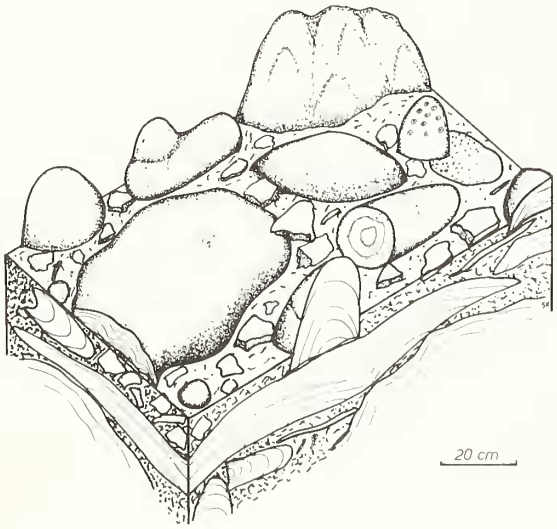
directing water currents through the structure to maximize feeding. This work is based on the well established Bernoulli's principle of water flow from high pressure, slow moving water near the stromatoporoid skeleton to low pressure faster moving water around the tips of protrusions (Vogel 1978).

Mamelons in the present specimens could have had a similar function, or as Kershaw (1981) suggested, caused turbulence close to the skeleton surface to assist feeding. The absence of astrorhizae on surfaces of many stromatoporoids does not necessarily negate a relationship with water flow, because in many modern calcified sponges the astrorhizal system exists entirely in the soft tissue coat and makes no impression on the skeleton. Nevertheless, in many stromatoporoids at Kuppen, and elsewhere in Silurian and Devonian rocks, there is a calcified astrorhizal system that is not associated with mamelons, and so the importance of mamelons in controlling water currents is questionable. Also, the presence of vertically orientated mamelons on sloping stromatoporoids suggest that other factors are responsible for mamelon development.

Suggestions have been made that stromatoporoids were photoresponsive. Kazmierczak (1969) proposed symbiotic ?algae, and also that stromatoporoids are themselves cyanobacteria (e.g. Kazmierczak and Krumbein 1983). Since only a few specimens of *C. mohicanum* have such protrusions, they are unlikely to represent a photoresponse in this case. Surface morphology of the biostrome was suggested by Kershaw (1981) to cause mamelon growth in hollows. Although surface depressions on the biostrome are not identifiable due to biostratinomic effects, their inferred presence could explain the specimens with mamelons. They are present in several localities and levels and consequently not limited to particular parts of the biostrome. They could therefore be a response to low energy causing an increase in stromatoporoid surface area and enhanced eddy formation for feeding in quiet spots. However, they cannot reflect increased sedimentation where they occur since the 'valleys' between mamelons only rarely contain sediment, and laminae of the stromatoporoid are continuous over the tops of mamelons and the valleys between them.

CONCLUSIONS

This study reveals two major growth styles in stromatoporoids in a low diversity assemblage, favoured by one species, in a low to moderately turbulent environment with a low sedimentation rate. Environmental gradients involving water turbulence and sedimentation appear to have played an important role in controlling distributions of species and growth forms. The abundance of low



TEXT-FIG. 12. Reconstruction of a small part of the lower biostrome, showing many stromatoporoids in life attitude, and taller forms overturned, plus fragments. Large, low profile shapes are based on *Clathrodictyon mohicanum*, and taller forms on *Plectostroma intermedium*. One specimen contains rugose corals, while an extended domical form on its side has continued to grow following overturning. A large domical form has developed by coalescence. Matrix is micrite, with skeletal debris.

profile stromatoporoids, in particular *Clathrodictyon mohicanum*, can be attributed to a number of factors including substrate colonization, stability of the substrate during times of higher energy, competitive ability, and coalescence, and is favoured by a low sedimentation rate. Most stromatoporoids in the suite grew on dead skeletal material, providing an important feedback to the living assemblage. Biostratinomic movement of skeletons, selective removal of taller growth forms and the pervasive effects of pressure solution, have distorted the life assemblage. A composite reconstruction of a small area of typical biostrome surface is shown in text-fig. 12, to illustrate the biostrome surface at an unspecified point in its development.

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